LITERATURE CITED —

Brewer-Carias, C. 1971. *In litt.*

Clayton, C. 1994. *Heliamphora* further explored. Bull. Austral. Carniv. Plant Soc. 13:12.

Jaffe, K, et. al. 1992. Carnivory in pitcher plants of the genus *Heliamphora* (Sarraceniaceae). New Phytol. 1 22:733-744.

Renner. S. 1989. Floral biological observations on *Heliamphora tatei* (Sarraceniaceae) and other plants from Cerro de la Neblina in Venezuela. PI. Syst. Evol. 163:21-29.

Oxygen budget in the traps of *Utricularia australis*

Lubomir Adamec
Institute of Botany of the Academy of Sciences of the Czech Republic. Section of Plant Ecology. Dukelska 145, CZ-379 82 Trebon. Czech Republic
tel. 0042-333-2522 fax 0042-333-2391

Suction traps of the aquatic bladderwort *(Utricularia)* species are 1-5 mm wide bladders, the walls of which consists of only two layers of cells (see Lüttge, 1983, p. 501-504; Juniper et al., 1989, p. 64-71). During suction of a prey (firing), their luminal volume is increased by more than 40 % (Lüttge, 1983, p. 502). In aquatic bladderworts, the light-green traps contain chlorophyll and are capable of photosynthesis. Frequently, older traps become pigmented and their colour is rose to black (Knight, 1992). How prey is digested in *Utricularia* traps remains unclear, although microorganisms were shown to play a role (Juniper et al . 1989, p. 195).

The small volume of the traps together with their respiratory activity and that of the prey may cause the prey to die from anaerobiosis as recently hypothesized by Dr. Laurie E. Friday (Cambridge Univ.. U K.). Direct evidence is, however, lacking. Animals caught in the traps may stay alive for a certain period: Hegner (1926) investigated feeding of *Utricularia* traps by protozoa and observed that they had died after 75 min.

The aim of this study was to evaluate the oxygen budget in *Utricularia australis* traps based on measured values of their photosynthetic and respiration rates.

Utricularia australis R.Br. was cultivated outdoors or collected from a fishpond near the town of Trebon (Czech Republic). Net photosynthetic rate (PN) and dark respiration rate (DR) were estimated in a closed stirred chamber (8.6 ml) at a temperature of 22° C as linear parts of current response of a fine O_2-sensor in 20-min periods of light or darkness. The irradiance was 70 W.m^{-2} (400-700 nm). The experimental solution contained 1.04 mM $NaHCO_3$ and 1 mM KCI. and had a PH of 7.4. Thus, the initial $C0_2$ concentration was about 0.1 mM. Three groups of mature empty traps of different age and colour (32-51 traps) were selected (Table I). The pigment responsible for the dark colour of the traps was a red anthocyanin as was shown in diluted HCl. In other experiments (Table II), DR of intact empty traps,

halves of these traps, and of traps with prey, was measured. Results are expressed on either a fresh weight basis (after pressing out the luminal solution) or per trap. Values are the mean of 2-3 replicates.

PN values of *U. australis* traps depended greatly on trap age and/or colour (Table I). On fresh weight basis, PN in the young light-green traps was five times higher than in the old dark-pigmented ones. However. only a twofold difference was found in *U. macrorhiza* traps of different age while the range of PN was about the same as in *U. australis* (Knight. 1992). DR related to the FW did not differ so much between the three colour groups, and when related to one trap, DR values were the same. The DR values found in *U. australis* traps (see also Table II) are within the range of those measured in *U. macrorhiza* traps (Knight, 1992) and are about 2-3 times higher than those in *U. purpurea* (Moeller, 1978) and *U. vulgaris* shoots (Draxler, 1973). This is probably due to a high energy consumption in traps necessary for pumping out water. However, the mean Pm values in *U. australis* traps (Table 1) measured at 0.1 mM $C0^2$ were about 2-4 times lower than PN in *U. purpurea and U. vulgaris* shoots at lower $C0^2$ concentrations. Knight (1992) found in *U. macrorhiza* that the PN of leaves was 2-3 times higher than that of traps. This demonstrates that *Utricularia* traps are considerably less efficient photosynthetic organs than the shoots. In *Aldrovanda vesiculosa,* the PN value of traps was 67 % of that of shoots (Adamec. 1993. unpublished). These findings confirm the common theory that carnivory decreases PN of organs (Juniper et al., 1989, p. 145; Knight, 1992). In halved traps when both trap sides were exposed to the external solution no increase of DR was found as compared to the intact traps (Table II). The DR values of traps with prey were surprisingly slightly lower than those of empty traps.

What can be concluded from the above data? Firstly, photosynthesis in the traps is very low but it is still present even in dark-coloured traps. Secondly, marked oscillations of O_2 concentration may occur in the luminal solution between night and day (L. E. Friday). This may be partly independent of the 0_2 concentration in the ambient medium. Model calculations of the night luminal 0_2 concentration follow. The above measurements show the 0_2 consumption from the external solution, mainly by the external trap walls and trap structures. However, it may be assumed that 0_2 consumption from the luminal solution by the inner trap side occurs simultaneously before the internal 0_2 pool is exhausted. The cardinal question is what is the ratio of the "external" and "internal" respiration rates when 0_2 concentrations inside and outside the traps approach a saturation level (ca. 9.0 mg O_2.1-1). Owing to certain symmetry of the trap walls, we can assume that the "internal" DR is at least 10 % of the "external" one measured. This is about 0.02 µg $O_2.h^{-1}$ in the case of a middle- aged, rose-grey, trap of a volume of ca. 2.51 µl (Table I; trap diam. 2.0 mm, trap width 0 8 mm). Such a dark respiration rate would reduce the internal O_2 concentration by 8.0 mg $0_2.l^{-1}.h^{-1}$. Thus, the saturation O_2 level of ca. 9.0 $mg.l^{-1}$ may be exhausted theoretically within 68 min. In smaller traps (vol. 1.78 µl; see Table II), the depletion of internal O_2 would occur within only 33 min.

Respiration activity of a possible prey was also taken into account. *U. australis* traps are able to catch only very small zooplankton species, e.g. *Chydorus sphaericus,* small *Bosmina* or ostracods. Dry weight of this kind of prey is about 2 µg (Jorgensen, 1979, p. 229-230) and their respiration rate is rather variable within 0.037-1.56 µg $0_2.h^{-1}.prey^{-1}$ at 20-26°C (Jorgensen, 1979, p. 250-252). In the traps stated in Table I (vol. 2.51 µl), the saturation level of O_2 should be exhausted by one prey theoretically within 0.9-37 min and the prey could die of anaerobiosis. However, in the traps stated in Table II, the prey (fine ostracods) survived in dim light or darkness at least for 8 h.

Experiments in Table II were performed to distinguish the "external" and "internal" DR. However, no increase in DR was found either in halved traps with both external and inner sides exposed to the experimental solution or in the traps with prey. These results contradict each other: the former treatment indicates that the internal 0_2 consumption by the intact traps is permanently compensated by 0_2 diffusion from the external medium whereas the latter shows that the luminal solution is isolated from the outside. All the traps studied were obviously after firing and were pumping out water. In any case, the speculations on the 0_2 concentration inside the traps cannot substitute for a direct measurement of 0_2 concentration by an 0_2-microsensor,

ACKNOWLEDGEMENT

Sincere thanks are due to Dr. Laurie E. Friday, Univ. Cambridge. U. K. for valuable suggestions and discussion.

Table I. Net photosynthetic and respiration rates of empty traps of different age and colour. The mean trap size was 2.0-2.2 mm and the width 0.8 mm. Mean fresh weight (FW) of a trap is given.

Age and colour of traps	Mean trap FW (mg)	Photosynthesis mg 0_2 g.h	Photosynthesis µg 0_2 trap.h	Respiration mg 0_2 g.h	Respiration µg 0_2 trap.h
young, light green	0.55	0.54	0.30	0.38	0.21
older, rose-grey	0.83	0.31	0.26	0.25	0.20
older. blue-black	0.87	0.11	0.09	0.25	0.22

Table II. Respiration rates of intact empty traps and of these traps after they had been halved. The young traps with prey contained each 1-2 small ostracods (ca. 0.6 mm) and some of the prey was still alive during the measurement. The mean trap size was about 1.8 mm and the width 0.7 mm. Mean fresh weight of one trap is given.

Type and treatment of traps	Mean trap FW (mg)	Respiration mg 0_2 g.h	Respiration µq O_2 trap.h
intact empty young traps	0.77	0.38	0.29
halved young traps	0.77	0.34	0.26
young trapswith prey	0.85	0.32	0.27

REFERENCES

Draxler G., 1973. Gaswechselmessungen an *Utricularia vulgaris.* In: Ellenberg H. (ed.), Okosystemforschung. Springer, Berlin, pp. 103-107

Hegner R. W., 1926. The interrelationships of protozoa and the utricles of *Utricularia.* Biol. Bull. 50: 239-270.

Jorgensen S. E. (ed.), 1979. Handbook of Environmental Data and Ecological Parameters. Pp. 1162, ISEM, Copenhagen.

Juniper B. R., Robins R. J., Joel D. M.. 1989. Carnivorous Plants. Pp. 353, Academic Press Ltd, London,

Knight S. E., 1992. Costs of carnivory in the common bladderwort. *Utricularia macrorhiza.* Oecologia (Berlin) 89: 348-355.

Lüttge U., 1983. Ecophysiology of carnivorous plants. In: Lange 0. L.. Nobel P. S., Osmond C. B., Ziegler H. (eds.). Encyclopedia of Plant Physiology, New Series. Vol. 12C Berlin-Heidelberg-New York, pp, 489-517.

Moeller R. E., 1978. Carbon-uptake by the submerged hydrophyte *Utricularia purpurea.* Aquat. Bot. 5: 209-216.

Southeastern CP Meeting Planned.....

Mark your calendars for the up coming Southeastern CP meeting hosted by Larry Mellichamp at UNC Charlotte. Lot of things are planned for this 2nd annual meeting. This year there will be a field trip to a local bog, talks on all CP's, and a plant swap and auction. As in the last year we will have a Friday night gathering to get to know the attendees. The meeting is set in Charlotte, NC on September 22, 23, and 24, 1995. All are invited and more will be mailed at a later date to the southeast area. If you wish to attend or help with this meeting please contact Larry Mellichamp at UNC Charlotte, DEPT. OF BIOLOGY, Charlotte, NC 28223 or Steve Baker, Rt. 1, Box 540-19AB, Conover, NC 28613, 704-256-7035. Hope to see you there.